ON *DENDROCINCLA TYRANNINA:* MORPHOLOGY, BEHAVIOR AND CONSERVATION OF A SHY LEK-TYPE INSECTIVORE

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Resumen

Willis, E.O. & Y. Oniki.: On *Dendrocincla tyrannina*: Morphology, Behavior and Conservation of a shy lek-type insectivore. - Caldasia **18**(86): 131-140, 1995. - ISSN 0366-5232.

El trepatroncos tiranino o "churulo" (*Dendrocincla tyrannina*, Dendrocolaptidae) de los bosques de neblina del norte de los Andes es solitario, como las otras especies del género. Se desplaza en el sotobosque lleno de epífitas, dependiendo parcialmente de los insectos que huyen de los escasos ejércitos de hormigas. Es un ave silenciosa y arisca, que se esconde después de volar cortas distancias en busca de presas, o procurándolas en musgos o troncos. La pérdida de los bosques húmedos andinos de laderas abruptas para dar lugar a la ganadería de baja productividad amenaza a la especie y aumenta el peligro de derrumbes en áreas sujetos a temblores; el uso más apropiado para tales áreas es para estudios científicos y actividades turísticas, y no para asentamientos permanentes.

Palabras clave: Morfología, Conservación, Ecología, Aves, Dendrocolaptidae.

Abstract

The Tyrannine Woodcreeper (*Dendrocincla tyrannina*, Dendrocolaptidae) of northern Andean cloud forests is solitary, like the rest of the genus, and wanders in the epiphyte-laden forest understory, depending partly on hard-to-find swarms of army ants and on understory flocks to flush insects. It is wary and silent, hiding after flying short distances for prey or gleaning it from moss or trunks. As loss of steep Andean wet forests where the woodcreepers live results in gretaer danger from earthquakes, study and tourism are preferable to settlements.

Woodcreepers of the genus *Dendrocincla* (Dendrocolaptidae) regularly follow swarms of army ants in neotropical forests, to capture flushed insects and other small prey (Skutch 1969, Willis & Oniki 1978, Willis 1972, 1979, 1983a). Females care for nests and eggs alone, and associate with males only briefly for mating.

Many birds with this behavior eat abundant fruit or nectar, not dispersed and hidden insects; indeed, Snow (1963) proposed that food abundance allows females to feed young without male help. More study of Furnariidae and Dendrocolaptidae is needed, for Skutch (1969) and others have noted some cases of females feding young alone in these insectivorous groups. Still, insectivorous female feeding young alone is usually considered to require explanation. Willis (1972) saw no evidence that food was abundant for dendrocinclas, suggesting that females feeding young without male help should be at a disadvantage. He tentatively suggested that attacks by larger woodcreepers over ants lead dendrocinclas to live solitarily, unlike pairing large birds that can defend sites large enough for male and female to forage together.

D. tyrannina, the Tyrannine Woodcreeper or "churulo" (on one Ecuadorean specimen label), is the largest species of the genus and occurs high in the northern Andes (1500-3200 m, locally lower in wet and cool Pacific forests) where there are few or no large competitors. In 1989 and 1991, we studied its behavior and sexual dimorphism, predicting that it might be monogamous due to "dominant" foraging conditions. To our surprise, it is a retiring and rare solitary species, males of which sing for hours each day in what could be "exploded" or dispersed leks. Our studies suggest a modification of BRADBURY'S (1981) hypothesis for the origin of exploded leks, which are likely to be the first step toward true leks (displays by grouped males). We also discuss other hypotheses for the origin of this behavior, as well as comment on conservation problems for this rare species due to widespread deforestation.

Methods

After unsuccessful searches at several likely forested sites out of Popayán, Colombia, we studied Tyrannine Woodcreepers from 10 February to 14 March 1989 at La Planada Nature Reserve (0° 54' N, 77° 16' W, 1800 m elevation) above Ricaurte, Nariño, Colombia. We used binoculars and tape recorder, noting behavior at each encounter with the species. In November, 1991, WILLIS found the species briefly at 2200 m by Km 66.5 (0° 2' S, 78° 42' W) above Mindo, Ecuador. Even with playback of tape recordings, he could not find it at sites under road construction nearer to Mindo, nor on the eastern face of the Andes from Cosanga (1900 to 2300 m) on the Cordillera de los Guacamayos, where J. Fjeldsa (pers. comm.) had found them a year or two before.

To determine which sex is larger, we registered weights and measurements from 34 specimens at La Planada, Universidad del Valle (Cali), Instituto de Ciencias Naturales of the Universidad Nacional (Bogota), and Louisiana State University (Baton Rouge): culmen from skull, bill height at anterior end of nostril, bill width at gape angle, tarsus, wing chord, and tail between central tail feathers. Culmen and wing measurements were available from 61 other specimens studied from 1970 to 1978 at the American Museum of Natural History (New York), National Museum of Natural History (Washington, D.C.), Carnegie Museum (Pittsburgh), Field Museum of Natural History (Chicago), Philadelphia Academy of Natural Sciences, Los Angeles County Museum, Phelps Museum (Caracas), British Museum (Tring), Stockholm Museum, Berlin Museum, Munich Museum, Leiden Museum, and Paris Museum.

Results

Morphology. The Tyrannine Woodcreeper weighs only 51.9 ± 5.3 gms (range 40-64, n = 34), less than the seemingly smaller but compact *D. obidensis* at Manaus, Brazil (Willis 1979). Females in Peru average lighter than males, 50.6 ± 5.1 g versus 53.7 ± 5.7 (n = 9,17), but the difference is not quite significant (p = 0.1). Males, overrepresented in museum collections, are somewhat longer-winged and -tailed than females, equatorial birds somewhat smaller than ones northward or southward (Table 1). The species does have a large "tyrannine" bill, long tail and wings, and a fluffy plumage that make it seem large. It is larger than *D. fuliginosa* of the nearby lowlands, a bird almost identical in color but for a narrow dark mustache and gray face.

Molt and breeding. Wing molt of males was recorded in March (2) and June in Colombia, tail molt in August; females were in wing molt in July, August and October. In Ecuador, male wing molt came in May and August, female in September (2). In Peru, females were ending molt in July, August and November, one male in November. One Venezuela male was ending molt in November, one Cundinamarca bird in mid-primary molt in December. The many other June to October birds seemed in good plumage, the few February to April birds in worn plumage (except Venezuela, where little worn). Molt seems to Center in the dry southern winter, except for birds well north of the equator. Tail molt starts with the central feathers as

Table 1. Measurements of tyrannine woodcreepers.

	Measurements[a]					
Country	**Wing**	**Tail**	**Tarsus**	**Culmen**	**Bill Height**	**Width**
Venezuela						
Male	127.2 ± 2.8(4)	-	-	36.7 ± 0.5(4)	-	-
Female	124.0 ± 1.4(2)	-	-	35.2 ± 0.1(2)	-	-
Colombia						
Male	124.5 ± 3.8(17)	110.6 ± 5.2(7)	25.1± 1.2(7)	36.6 ± 1.3(20)	7.6(7)	14.1(6)
Female	119.0 ± 3.0(14)	103.5 ± 0.7(2)	25.1 ± 0.1(2)	34.7 ± 1.5(16)	7.2(2)	13.7(2)
Ecuador						
Male	120.2 ± 2.8(8)	-	-	36.1 ± 1.8(11)	-	-
Female	118.0 ± 5.0(3)	-	-	35.0 ± 1.8(4)	-	-
Perú						
Male	126.5 ± 2.3(25)	115.5 ± 2.6(17)	25.7 ± 0.6(17)	37.7 ± 1.4(25)	7.7(16)	14.3(17)
Female	123.0 ± 3.0(9)	113.9 ± 4.3(9)	25.8 ± 0.9(9)	36.9 ± 1.0(9)	7.7(9)	15.0(9)

[a] x ± s.d. (n).

the middle primaries drops. Birds with black bills (perhaps inmatures, as in other Dendrocolaptidae) were from June on Munchique and in Valle, April in eastern Ecuador, and (ovary enlarged, perhaps nearly one year old) February in Venezuela. The Valle bird was registered as an immature by the collectors (G. Cataño & J. I. Borrero, Univ. Valle) but was ending wing molt, perhaps nearly a year old. Enlarged gonads were recorded for several birds in October-November in Peru (LSU).

Antipredator behavior and foraging. It took us a week to see our first Tyrannine Woodcreepers at La Planada, despite good trails through the forest and daily searches. The first lone bird (Oniki) hitched up saplings 5-10 m up, stopping to look around, then flew to a large trunk and circled behind epiphytes, disappearing. This silent and evasive behavior was typical of birds seen later, making it almost impossible to follow them. Other dendrocinclas are more conspicuous, calling sharply before disappearing behind trunks or flying off directly.

Typically, the birds observed favored small and relatively epiphyte-free trunks. They were able to hitch up or pause in dense "moss" or lichens, however. Most were 2 to 15 m up in the understory of epiphyte-laden forest or tall second growth. Only the Mindo bird came close to the forest edge, and it soon flew back in the forest patch between the road and intersecting landslide zones. J. Fjeldsa (pers. comm.) has seen it in semicleared areas, but this behavior, if frequent, would have put it into view of many ornithologists.

Several individuals, including the Mindo bird, were following in or under low or midlevel mixed-species flocks of tanagers, wood-warblers and other birds, sallying out now and then to capture falling prey or small items on the trunks, moss, or epiphytes. Unlike *Lepidocolaptes affinis* pairs in the flocks, the species does not climb trunks pecking or probing into epiphytes of the bark. It does not rummage in epiphytes or tree crotches, unlike *Xiphocolaptes promeropirhynchus* at the same elevations. Instead, like other dendrocinclas over ant swarms, it waits and then sallies for distant food, or moves upward or onward a short way to a new site. Most mixed flocks lacked the species, or it hid when we appeared.

Several individuals, like the first one, were wandering alone and away from flocks. One fluttered and clung below a mossy spray of foliage, pecking into the moss with the bill. K. Schuchmann (pers. comm.) saw one scratch moss off a twig with one foot, but the bird fled when it saw him.

Only one bird followed a swarm of the army ant *Labidus praedator*. It worked low among other birds, sallying to the ground or to foliage to 5 m up for over and hour at midday, then hid behind a small low trunk and preened quietly for 10 minutes as ant activity ceased. While swarms of this ant were fairly common at La Planada, one had to almost step on the ants to see them in the gloom amid deep litter and mossy trunks. Several swarms had attendant birds, although by 9:00 or so a few brush-finches (*Atlapetes brunneinucha*), woodwrens (*Henicorhina leucophrys*) or orther casual ant-followers were often present. If the Tyrannine Woodcreeper is wandering alone or in mixed flocks to search for ants under La Planada conditions, it probably would do better to wait until other birds have located the ants in the morning.

All *D. tyrannina* seen were alone. F. G. Stiles and L. Rosselli (*in litt.*) have now banded a male and female (by measurement) in a 14-ha area under study at 2800-3100 m in the Eastern Andes near Bogota; the birds have always been seen singly (although often with mixed flocks), despite some overlap in areas of use. (They have not seen army ants in their study area). While one often sees isolated individuals of pairing species of woodcreepers, one usually sees pairs together some of the time. Since no other dendrocincla forms pair bonds for more than a short time at mating, and females care for nests and young alone, we conclude that our initial prediction of monogamy in *D. tyrannina* was incorrect.

Singing behavior. On 4 March, Willis climbed the ridge north of the forested plateau at La Planada, and was surprised by a loud song that reverberated down the ravine every minute or two. Playing back a recording quickly brought up a single Tyrannine Woodcreeper, which flew past twice and gave a few "tee-tee-tee-teet" sharp calls, then lost interest and wandered off to sing. Every morning to 14 March, a bird sang on this ridge near a small notch, its voice amplified by the small ravine down either side as if by a megaphone, from first light at 05:59 or so (the first bird after potoos and owls) to 9 or 10 a.m. Occasionally one gave a song or two to 11:00 under a bird flock to 500 m off along the ridge, but playback seemed to scare it off. It sang again from 18:15 or so to dark at 18:40 hours. The song was so loud that, once we learned it, we could hear it from the laboratory a kilometer or so off, and from about the same distance northwest across the curve of the ridge.

After we played the song for other ornithologists, students remembered hearing the song, perhaps from two birds, on the similar ridge south of the laboratory. Willis verified that one bird with a slightly different song ending sang at the end of that small ridge every morning, ending about 08:30. He tried playback to the south and north singers after setting up mist nets, but the birds flew over the nets once or twice and went back to singing.

On different mornings, we checked ca. 3 km along the ridge around La Planada, but only these two sites away from open pastures at the east were in use. Occasionally we heard a few songs out on the plateau during the day, but the songs were never repeated at other visits and playback attracted no birds. We never got any response to playback at the song areas on the ridges outside of singing hours.

The song, as recorded at La Planada and in Ecuador 07:00 on 17 March 1987 at 2000 m above Tandapi, P. Coopmans; used by J. W. Hardy in his cassette recording of woodcreeper voices), is a series of 90 or so notes, starting faint and slow, accelerating and getting louder until one's ears ring. One song analyzed was 12.6 seconds long, counting seven faint introductory notes in 1.7 seconds and two faint end notes in 0.5 second; notes in the main song came at 8-9 per second and increased in frequency from 2 to 2.3 kHz, with reverberations from trunks forming a smudge after each note (Fig. 1). The bird's body shakes with the force of the notes, head out from the trunk and crest and throat slightly ruffed. During intervals, it looks about with crest somewhat raised, wipes one side of the bill, flicks the wing tips a bit, or hitches a short way up the trunk. We never saw it forage in the song area.

Intervals between the ends of songs peak about 40 and 90 seconds (Fig. 2), but intervals can be longer, especially when the bird changes perch after a few songs. Though intervals of 80 or more seconds were often linked with obvious moves (24 of 38 moves), there were 43 other intervals of over 80 sec. when the bird did not move long distances, perhaps on the lookout for predators. Long intervals became more frequent after 08:00 (22 of 57 intervals versus 15 of 97 before 8:00 on March 5, $X^2= 6.19$, $p<0.05$); moves became more frequent after 7:20 a.m. (4 in 50 minutes before, 12 in 75 minutes after). Moves were unpredictable; on March 5 being after 4-4-7-22-3-2-4-3-14-13-10-3-10-12-26-3 songs; long intervals were also irregularly inserted, every 7-8-11-12-4-3-3-2-4-3-14-4-1-3-5-10-1-3-6-3-1-4-2-5-1-1-1-1-5-1-3-6-3-1-3-2 songs. Although sequences of 9 and 11 songs came at intervals of 44 to 54 seconds, unpredictability of interval was more the rule.

The singing bird moves back and forth along one side of the ridge, shifts to the other side, and is cautious, hiding behind a trunk or freezing with crest up and a flit or two of the wing tips at

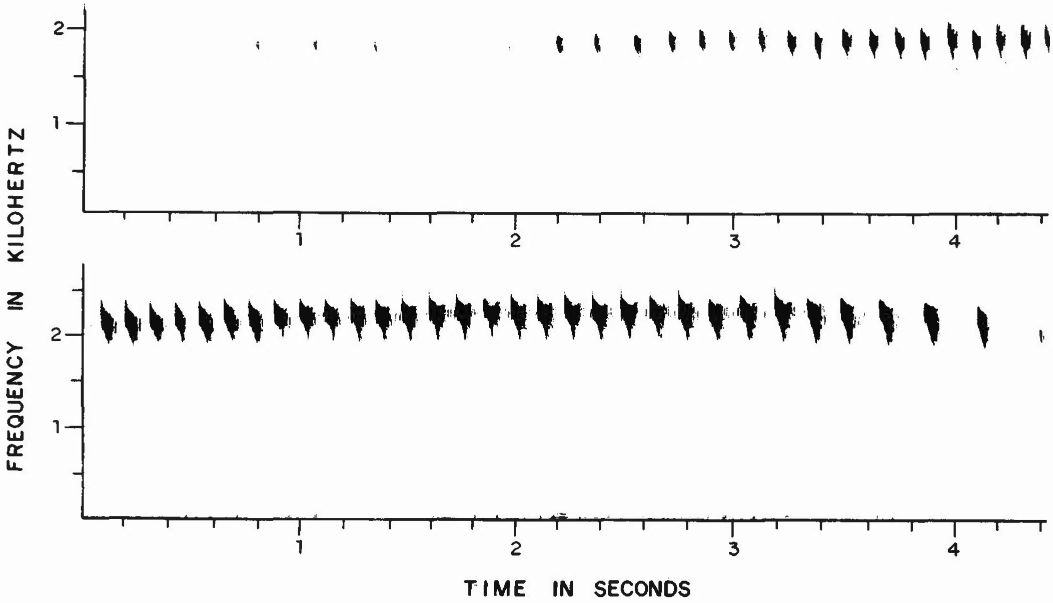

Figura 1.

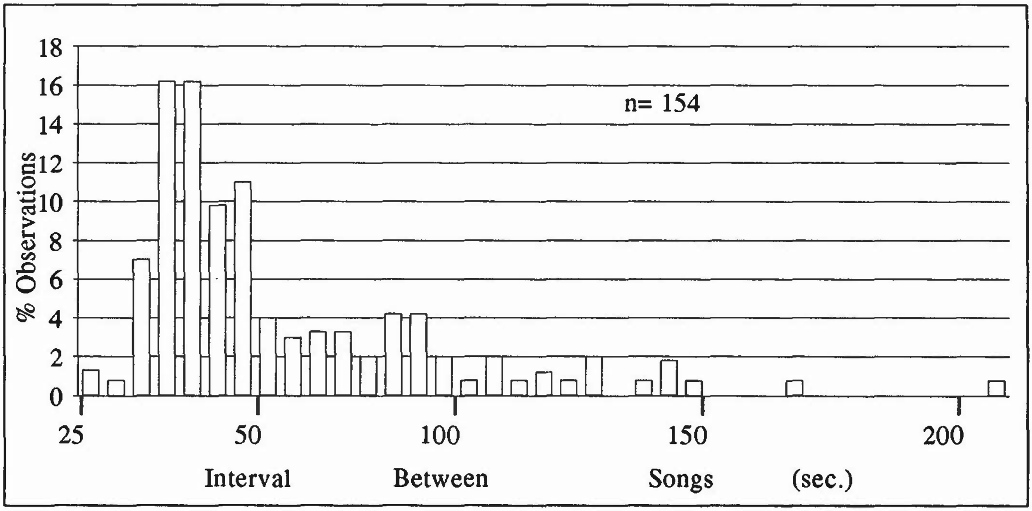

Figura 2.

any disturbance. It tends to sing at the high extreme of the foraging range, 5-15 m up, or to 20 m in the subcanopy for the south bird. Foggy or drizzly days do not stop singing.

In November 1991, Willis heard no songs at all at dawn or dusk at the many Ecuadorean sites visited, even with playback. Howeber, the rains had not started and the birds may not have been breeding. P. Coopmans (in litt) attracted a bird from a mixed flock with playback on the misty afternoon of 14 November 1988.

Discussion

D. tyrannina seems closely related to *D. fuliginosa*, the main morphological differences being a larger bill to get prey out of moss and lichens on upland trunks, larger size and fluffier plumage for cool climates, long tail for lichens, and long wings for more wandering where ants are rare (or related to body size). It is even more plain brown in color, perhaps for concealment.

In general, behavior differs little from lowland dendrocinclas. It is a solitary, wary bird that probably could move into the ant-poor highlands because presumed lowland ancestors were already used to low prey densities, being subordinate and peripheral wanderers at swarms. The main change from other dendrocinclas is loud adversiting for several hours daily at a special area. Female *D. fuliginosa* sing loudly at times anywhere within exclusive territories, while males wander in areas that overlap with each other and with several females (Willis 1972). K. Schuchmann (pers. comm.) found a nest-building female singing repeatedly, perhaps to attract a male. Male *D. obidensis* sing more than females, but more study is needed (Willis 1979). Stiles & Rosselli (*in litt*), based on wing and tail measurements, recently report male *D. tyrannina* using "a series of song perches within 300 m or so" in their study area and at La Planada. If females sing, they should do so only in pre-nesting weeks. Male singing indicates a social system similar to "exploded leks" or near-monogamy in Helmeted Menakins, *Antilophia galeata* (Marini 1989, Marini & Cavalcanti 1992). Singing *D. tyrannina* probably lose little foraging time because finding ants or following flocks is difficult before other birds accumulate, by 9:00 or so.

Could the advertising be territorial song? No other woodcreepers, except the probably nonpairing *Xiphorhynchus guttatus* in Panama (Willis 1983b), sing persistently from one area every morning for weeks. Also, the birds seemed relatively nonterritorial outside of song hours. Another explanation might be that, with considerable isolation of the La Planada reserve in recent years, local populations were low and birds could not find mates. However, use of special sites on rideges suggests a fixed behavior pattern, not a new response. In any case, the song pattern and sexual separation suggest Helmeted Manakins or other primitive lek species, such as the Stagemaker (*Ailuroedus dentirostris*) of Australia.

Fear of following. We now doubt our previous ideas on evolution of "promiscuity" in dendrocinclas and other species (Willis 1972, Willis *et al.* 1978). Avoiding females because they compete for food or become aggressive to do so seemed reasonable in earlier studies, especially since females of medium-large woodcreepers harass their mates but stay with them (Willis 1982a, 1992). Snow (1963) had even suggested the reverse of competition, that abundant food allows males to be released from nesting chores; but this idea seems incorrect for woodcreepers, where the large species with abundant food are very monogamous or even form trios with grown offspring (Willis 1982b). Bradbury (1981) suggested a more likely hypothesis: food can be rare, or abundant but scattered for the real problem is that a female that moves long distances can't be kept on territory, while a smart male can intercept her and several others at crossroads or "hotspots".

Ornithologists have mostly accepted Bradbury's idea, confining themselves to discussions of why displaying males should group together in true leks (the "hotspot" idea of Bradbury versus the "hosthot" one of Beehler & Foster 1988: that males flock around a superstar who attracts females). Stiles & Wolf (1979) had earlier proposed that, in hummingbirds, males are difficult for females to locate unless (a) they hold territories in conspicuous flower patches or (b) sing loudly, often in groups, when using scattered flowers. This "gunshot" or "lotspot" hypothesis would seem to be a third possible explanation for conspicous displays or songs. We return to this idea below. First, however, we indicate one major flaw in Bradubury's hypothesis: tanager, parrot, pigeon, antbird and other females that wander widely for fruit or ants are monogamous, the male simply following one rather than keeping her on his "farm". Moreover, many colonial or semicolonial birds, from albatrosses and herons to thrushes and icterines, have female movement without promiscuity; the female avoids sex, as if in another world (Howard, 1940), when foraging and accosted by a male without nesting property. In these species, of course, the male way have to protect the nest site, material, clutch, or offspring from neighbors, parasites or predators when the female is away.

What, then, keeps males from following faithless females? Here the shy dendrocinclas give a possible answer: in cluttered or closed habitats, sit-and-wait predators get the "second bird in line" if there is no cover close or flight speed is low. Following females is dangerous, especially for long distances in certain habitats. Once males are unable to protect females from extra-pair copulations by either territory or following, they might as well join the ranks of the "surplus" and promiscuous males.

Stiles & Rosselli (*in litt*) did not note avian predators inside forest in their study area above 2800 m, near the upper limit of *D. tyrannina* range. At La Planada, both *Micrastur semitorquatus* and *M. ruficollis* call morning and eve. There probably are many predators in most Andean forsts, for birds are wary. Lack of predators may follow local isolation of forests, however.

Two additional considerations are necessary. If the male has to stay on white eggs part of the day, as in pigeons, wall the female up to protect his nest, as in hornbills, or protect the nest in a colony (above), neither the male nor female can forego monogamy. Mock & Fujioka (1990) review recent literature along these lines, emphasizing the basic idea of male help in feeding young. We suspected that inter or intraspecific nest parasitism, predation, or robbing of material is more often the reason. Second, Snow's idea of food abundance may explain display increases after monogamy is lost. Abundant food gives the male time to sing and dance, difficult for an insectivore that has to forage most of the day. However, food abundance without female movement creates dense territories, and female movement without male fear of following creates "lovebird" parrots.

Finding females. Stiles (*in litt.*) suggests a possible reason for conspicous displays in insolated males, based on Stiles y Wolf (1979) : finding females. This is not an alternative to "fear of following", which is related to loss of monogamy; it is a second step, after monogamy is lost and before lek groups form. Male woodcreepers would already be nonpairing birds, either from fear of following or from food abundance at ant swarms (Snow's hypothesis, which we rejected above). We agree that, in dendrocinclas (as well as in their probable relatives, genus *Sittasomus*), females always care for nests alone; and that *D. tyrannina* may simply never have developed pair behavior. (We consider that fear is a good reason for not returning to monogamy). Stiles suggests that lack of ant swarms to concentrate dendrocinclas in the Andes may have made it necessary for *D. tyrannina* to sing loudly, for male to find a female or vice versa. He notes that at their high-elevation area, bird flocks are often followed, as at La Planada, but may not be enough for male and female to find each other rapidly at the start of nesting. There are more ant swarms at La Planada, but all are of the hard-to-find *Labidus praedator* or similar species, not of *Eciton burchelli* where raids and birds of the opposite sex are easier to find.

If the "finding females" hypothesis is correct, loud voices and conspicuous displays in certain areas should arise mainly in closed or cluttered habitats where rare birds cannot be seen at a distance. This prediction is the same as for "fear following", except that birds need not be rare. Since lek-forming manakins and cotingas are often very common (Snow, 1963), it may be that finding females need not be difficult (except in such birds as dendrocinclans and forest-interior small hummingbirds). Cluttered predator-rich habitat, however, is normal for lek or court-forming birds all over the world: bustrads, ruffs, woodcock, grouse, birds of paradise, manakins, cotingas, hummingbirds, and now woodcreepers. Birds that fly in the canopy or open are territorial pairers or follow their females.

Conservation. We doubt that Tyrannine Woodcreepers, which already occur at such low densities that they sing to be heard a kilometer off, can find enough food or cover from predators in the pastures with scattered trees that are taking over the Andes. One was caught in a dark hallway at the university in Popayán some years ago (Museo de Ciencias Naturales specimen), but where else could a forest-interior bird hide when its dark forests were cut?

Increasing human populations, firewood cutting, and the poor people one sees in dry interior cities like Quito and Popayán are not the problems. Wet forests where the species lives give a little lumber for rich homes and a bit of tapir meat (Cosanga), but are mainly being turned into nearly empty cattle pastures for affluent weekend owners from the city; we saw almost no use of *D. tyrannina* zones for food crops or settlements.

However, poor people often cut forests under pretense of homesteads of "land reform", for money can always be made selling cleared land and moving on to cut more free government forest. To stop the spread of Latin rich yearning to be on horseback, some conservation groups now buy land near reserves with rich foreigners' money and turn the land over to government or private park units.

Forests, cattle, and people on the back side of Reventador Volcano northeast of Baeza had been destroyed for miles by an earthquake a few years back, suggesting that habitat for birds like the woodcreeper may be destroyed locally every hundred years or two. Single reserves in earthquake and volcano zones can be destroyed overnight, something conservationists should remember. We recommend that most steep Andean zones, too dangerous for permanent settlement, be turned over to science and tourism if people are serious about "humanitarianism". New scientific ideas can come even from backwoods birds like woodcreepers.

Acknowledgements

We thank the National Geographic Society for support, ALVARO NEGRET of the Museo de Ciencias Naturales in Popayán for help, and the Reserva Natural La Planada staff, especially GUILLERMO CANTILLO, for their constant help in a rainy environment. DOUGLAS WECHSLER and VIREO provided illustrations and information on captured birds, J. W. HARDY & P. COOPMANS information on recordings, P. COOPMANS & J. FJELDSA information on observations in Ecuador, F. G. STILES & L. ROSSELLI on continuing studies in Colombia, and J. VIELLIARD a sonagram. We appreciate P. MESA's preparing the "Resumen" Curators at the many museums were always helpful. F. G. STILES and an anonymous reviewer suggested many helpful changes in the manuscript.

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